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FIELD BEHAVIOR AND SEASONAL ACTIVITY OF THE RODENT BOT FLY, *CUTEREBRA TENEBROSA*, IN CENTRAL WASHINGTON (DIPTERA: CUTEREBRIDAE)¹

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ABSTRACT.— Behavior and activity of the rodent bot fly, *Cuterebra tenebrosa* Coquillett, was studied at a natural aggregation site in central Washington. Daily flight activity extended from 1700 hr to 2030 hr (PDT) beginning in mid-July of 1970 and 1971. The peak of flight activity, in August, was followed by a decline in activity through September. Male flies aggregated on the vertical faces of basalt cliffs, where they awaited females. Daily activity reached a peak at temperatures of 30-35 C. Eggs were laid in rock crevices without regard to the proximity of *Neotoma* wood rat hosts. Developing fly pupae were found in litter in wood rat tunnels in basalt cliffs.

Adult bot flies are rarely encountered in nature, and their general behavior was little known until recent years. Most early information was gathered from scattered accounts of one or two flies captured during the warm months, and specific identification was often impossible due to lack of adequate keys. The first in-depth study of adult *Cuterebra* activity and behavior was by Catts (1967), who worked with *C. latifrons* Coquillett in California. Adult *C. polita* Coquillett activity at aggregation sites in Utah was studied by Graham and Capelle (1970) and Capelle (1970). Recently, Hunter and Webster (1973) reported behavioral studies of *Cuterebra grisea* Coquillett and *C. tenebrosa* Coquillett in British Columbia.

Very little additional information is available on the activity of *Cuterebra tenebrosa*, a large black cuterebrid whose larvae parasitize *Neotoma* wood rats in the western United States and western Canada. Parker and Wells (1919) obtained a female in September in Montana, and Moilliet (1950) reported the capture of a female in British Columbia in August.

During 1970 and 1971, adult *C. tenebrosa* were studied at natural aggregation sites in central Washington. The purpose of this paper is to describe: (1) seasonal and diurnal occurrence of adult *C. tenebrosa* at aggregation sites, (2) flight activity and mating behavior, and (3) oviposition activity and sites.

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MATERIALS AND METHODS

Field observations were conducted at the Columbia National Wildlife Refuge, Othello, Washington. The area is largely composed of rock slides and 15-35 m high basalt cliffs (Fig. 1A) with sagebrush and dry land grasses the main vegetation. Despite the overall dryness, a number of small streams and lakes exist in the lower areas (Fig. 1B).

Observations were made intermittently during all months of the year; however, the main attempts to study fly activity were between April and October of 1970 and 1971. Searches for aggregation sites



Fig. 1. General view of area where *Cuterebra tenebrosa* is active in central Washington. A. Male flies station themselves on the vertical cliff faces (arrows) to await females. B. Several aggregation sites (arrows) are visible in this view of the Columbia National Wildlife Refuge near Othello, Washington.

covered approximately 41 square kilometers (16 square miles) of the refuge. Intensive observations were confined to three aggregation sites, and nine additional sites were used for comparison.

Because of difficulty in collecting wild flies for release and resighting, only laboratory-reared flies were used for this purpose. They were marked on the mesonotum with white ink and released within two days of emergence. Marked flies were released under favorable weather conditions between late July and mid-August of 1971. Flies were released in shaded areas at the base of cliffs. Resighting and identification of individuals was possible with field binoculars (7x) from a distance of 10 m or less.

RESULTS

AGGREGATION SITES.— Adult *C. tenebrosa* were found on the vertical faces of basalt cliffs (Fig. 1A), rarely on top. Twenty-five different cliffs or rock formations were examined for activity during 1970 and 1971, and all had active *C. tenebrosa* on them at one time or another. As might be expected, some sites were better than others, as indicated by greater numbers of flies. The best sites were the east- and southeast-facing cliffs. These supported the greatest number of flies, whereas north- and west-facing cliffs were as a rule without *Cuterebra* activity. Smooth, brush-covered hilltops equal in elevation to the basalt cliffs were examined for fly activity, but no flies were found. Apparently they preferred the rocky, vertical sites.

During inclement weather and periods of inactivity, adult flies crawled into protected crevices in the vertical rock walls where they remained immobile until favorable conditions existed.

LONGEVITY OF ADULT FLIES.— Based on the release of marked flies, longevity in the wild is estimated at 5-9 days. In the laboratory, flies lived 8-13 days at room temperature (22 C) but were kept alive as long as 37 days at 4-6 C.

Resighting of marked male flies occurred as late as the ninth day after release, but for most flies 6-7 days was the maximum. Fourteen of 25 marked flies were resighted on subsequent days but only at the site where release took place. Although the three release sites were about 100-150 m apart, no interchange of marked males between sites was observed.

Only two of eight marked females were resighted. One was sighted on the sixth post-release day approximately 75 m from the release site as it investigated rock crevices in an apparent search for oviposition sites. The other female was seen on the fourth day as it rested beneath a rock overhang. It was within a few meters of the original release site.

SEASONAL AND DIURNAL ACTIVITY.— *C. tenebrosa* adults were active in the wild from July through September. In spite of regular searches of the study area beginning in April 1970, flies were not observed until 23 July 1970. In 1971, flies were first observed on 10 July. Following the first sighting in each year, adult flies were

active on favorable days into late September. The last fly to be sighted in either year was on 8 October 1971.

Dr. Charles L. Graham, who has examined *Cuterebra* specimens and label data from major United States collections, reported that *C. tenebrosa* activity begins in mid-July and reaches a peak in August. Activity declines in September, but a few *C. tenebrosa* have been captured in California as late as October (personal communication, 1972).

In July and August of 1970 and 1971, fly activity at aggregation sites extended from 1700 hr to 2030 hr Pacific Daylight Time (PDT). More flies were seen on days when the air temperature was 30-35 C, although some activity was observed at temperatures as low as 24 C. Flies remained in protected areas at temperatures below 21 C and were reluctant to fly. Weather conditions strongly influenced activity. During cold or wet periods flies were inactive. Heavy wind even on hot days curtailed flight activity, whereas light wind 16-25 km/hr (10-15 mph) had no apparent effect. On days of peak fly activity, the air temperature changed little from mid-afternoon until after flight activity ceased.

Male flies appeared at aggregation sites earlier (1700 hr PDT) in the day than females (1800 hr) and in greater numbers. Five to seven males were active at each site on favorable evenings, whereas only an occasional virgin female was sighted. Since the sexes are similar, they were distinguishable from a distance only by behavioral differences. Males usually perched on vertical rock faces in a head-up or a head-down attitude and pursued other insects including other *C. tenebrosa* males. Marked laboratory-reared flies were resighted many times but were never observed to dislodge a resident male. Numerous pursuits lasting from 3 to 10 sec always resulted in the resident male's returning to his perch. Pursuit occasionally took place above the cliffs but was usually confined to the top one-third of the cliff within 1-3 m of the rock wall.

Virgin females did not linger at aggregation sites for more than a few minutes. Their flight was direct without apparent searching behavior characteristic of gravid females. Virgin females were readily pursued by waiting males. Males overtook and coupled with females and then fell to earth, where copulation was completed. Mating was observed on two occasions in the wild, and in both cases it was completed in 10-15 min. Laboratory-reared flies that were handheld or confined to petri dishes averaged 32 min per mating (30 matings).

OVIPOSITION.— Gravid females were recognizable by their short flights from one crevice to another in search of oviposition sites. The earliest a gravid female was sighted was 1700 hr PDT in July; the latest was at 2115 hr or about 45 min after the last male was observed at the site.

After alighting near an opening and walking in, females remained inside for 5-10 min and then emerged to continue their investigative behavior. The flies seemed to prefer dark openings.

Most crevices and dark openings in the rocks were visited by ovipositing females, often by more than one fly. Preference was not shown for crevices and tunnels with active wood rat nests. Close examination of several crevices revealed *Cuterebra* eggs about 30-40 cm in from the entrance. These were laid without regard for the presence or location of a wood rat nest. Eggs were usually located on vertical surfaces singly or in groups of four to eight and were apparently laid as the fly entered. *Cuterebra* eggs were not found on nest materials or within 30 cm of any of 30 wood rat nests that were carefully dismantled and examined.

Egg capacity of 18 laboratory-reared *C. tenebrosa* females averaged 1870 (1462-2137), whereas gravid females captured in the wild averaged only 1270 (450-1460). This is probably a result of the flies' having already laid part of their eggs.

FLY PUPARIA IN WOOD RAT NESTS.— Twenty-two of 30 wood rat nests examined between May and August 1971 contained *C. tenebrosa* puparia. Twelve had viable pupae, 17 had empty puparia, and one nest had both. Puparia were found in the nest litter 5-20 cm below the nest proper. Gregson (1950) reported finding "shells of cuterebrid puparia" around wood rat nests.

DISCUSSION

AGGREGATION AND FLIGHT BEHAVIOR.— The occurrence of *C. tenebrosa* flies at elevated aggregation sites further points out the tendency for bot flies to concentrate at such locations. *Cuterebra tenebrosa* males utilized the vertical cliff walls for waiting sites rather than the actual cliff top. Townsend (1935) captured males of several *Cuterebra* species on bare hilltops and at upper end of ravines, although he made no mention of these sites as being for aggregation or mating purposes. Catts (1967) found male *C. latifrons* at hilltop sites between 0700 hr and 1200 hr (PST) from June to October in California's coastal mountains. Capelle (1970) and Graham and Capelle (1970) studied *C. polita* on south-facing hillsides in Utah where 30-40 flies (90%+ males) were active between 0930 hr and 1230 hr (MDT) on a given day. The *C. polita* flight season lasted only from late July to late August. Observations by Hunter and Webster (1973) concerning *C. tenebrosa* contrast with the present study in two ways: (1) The flies utilized the base of west-facing cliffs in British Columbia, whereas the same species aggregated near the upper portions of south- and east-facing cliffs in Washington. (2) The daily activity period was during late morning in British Columbia; in Washington, flies were active only in late afternoon.

Near Tucson, Arizona (Sabino Canyon), I observed an unidentified *Cuterebra* species active on 19-21 April 1969 on cactus-covered hilltops. We captured 11 males as they perched on prominent plants or rocks in an apparent watchful attitude, but the females were never sighted. Two days later, five males of the same species were taken from a rock-and-brush-covered hilltop near Congress, Arizona.

In these instances, all *Cuterebrid* activity was observed between 0800 hr and 1230 hr (MDT).

The abundance of *Cuterebra* males in relation to females is probably due to the females' being present at the site only long enough to be mated and the males' spending their entire lifetime there.

MARKED FLY RELEASE.— Marked flies were released to determine their longevity in the wild and to determine the extent of their travels. The longevity of 5-9 days is similar to the 10-day lifetime for *C. latifrons* (Catts 1967). Catts reported that only 1-2 percent of released flies moved from their original hilltop, an indication that males tend to occupy one aggregation site for their entire life. *C. tenebrosa* also tended to stay at one aggregation site.

Since resident *C. tenebrosa* males were not marked, identification of individuals was not possible. Therefore, territorial activity cannot be positively attributed to this species. On the basis of many observations, however, I believe the males do defend an area or territory against intruders as was described by Catts (1967). Marked laboratory reared flies were pursued by a resident male when they entered the primary activity area; at no time was a marked fly the established defender. Hunter and Webster (1973) observed *C. tenebrosa* males flying in an oval or figure-eight pattern over a 10-15 m long territory. Capelle (personal communication, 1973) offered an alternative opinion of male pursuit activity, suggesting that it is investigative mating behavior.

DIURNAL ACTIVITY.— *Cuterebra tenebrosa* appears exceptional in its late-afternoon and evening flight period. Other cuterebrids are morning or midday fliers (Catts, 1967; Capelle, 1970). Only one *C. tenebrosa* specimen was observed during morning hours. It was sighted at the base of a cliff at 0900 hr and probably had emerged that morning. Grunin (1959) indicates that members of Oestridae, Hypodermatidae, and Gastrophilidae generally are active during morning hours.

The intense heat of summer afternoons and evenings was not a deterrent to *C. tenebrosa* activity as it appears to be with morning-flying species. The stimulus to flight activity was not determined. Light intensity may be a factor, because at onset of fly activity (1700 hr) the east-facing cliffs were shaded although the air temperature remained at 30-35 C. Approaching darkness was the apparent terminating stimulus, although ovipositing females were active on windless evenings until complete darkness.

OVIPOSITION.— For many years it was assumed that *Cuterebra* flies oviposited on their host. Dalmat (1943) disagreed and suggested they lay eggs in the immediate host environment. Findings of Beamer et al. (1943) supported Dalmat's suggestion when *C. beameri* Hall eggs were found at the entrance of wood rat houses. Beamer (1950) observed *C. buccata* (Fabricius) females ovipositing on grass stems along rabbit runs. Catts (1967) found *C. latifrons* eggs on sticks around the entrances to wood rat houses. Graham and

Capelle (1970) observed female *C. polita* investigating pocket gopher burrows whether the burrows were actively being used or not. They suggested the stimulus for egg laying may be visual rather than olfactory. Capelle (1970) carefully excavated gopher burrows from which *C. polita* had just emerged and found eggs on the fine roots hanging from the ceiling. Although most *Cuterebra* have not developed host finding to this degree, it appears that oviposition in the immediate area of the host is the general pattern. *C. tenebrosa* females laid eggs in almost any site involving a dark hole or crevice. The visual stimulus seemed to be important. Host activity was not evident except in a few oviposition sites.

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